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A NEW GEOMYS FROM THE VALLECITO CREEK PLEISTOCENE OF CALIFORNIA

With Notes on Variation in Recent
and Fossil Species

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A NEW GEOMYS FROM THE VALLECITO CREEK PLEISTOCENE OF CALIFORNIA,

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and fossil species

By JOHN A. WHITE¹ AND THEODORE DOWNS²

INTRODUCTION

The Vertebrate Paleontology Section of the Los Angeles County Museum has carried on extensive field operations during the last three years in the highly fossiliferous badlands of the Vallecito Creek valley of the Anza-Borrego desert in the western Imperial Valley of southern California. A preliminary report on the varied Middle Pleistocene vertebrate fauna collected from this area has been presented (Downs, 1957), and a complete study of this fauna, and related stratigraphy, geology, and paleoecology, is in the process of preparation.

One of the species best represented in the fauna is a pocket gopher of the genus *Geomys*. Approximately 75 well-preserved portions of skulls and mandibles of this gopher are present in the collection. So adequate a sample as this provides an unusual opportunity for the paleontologist to derive more biologically realistic conclusions than are usually possible in his studies. This paper, therefore, is not limited to a description of the species represented by this fossil material, but includes: (1) analyses of the relationships of the fossil species and other known forms of *Geomys*, both living and extinct; (2) comments on possible paleoecological inferences, particularly with regard to the importance of intraspecific variation in paleozoological as well as neozoological studies.

ACKNOWLEDGMENTS: To Harley J. Garbani we are grateful for the discovery of the fossil-bearing strata in Vallecito Creek and for his enthusiastic aid in the field.

Although Downs initiated the study of the Vallecito Creek fauna in 1954, grants from the National Science Foundation (G-5035) to the Los Angeles County Museum Associates, in 1958 and 1960, provided him the means for more accelerated furtherance of the project.

The field work was made possible by the support and cooperation of the Department of Beaches and Parks, State of California, especially the management and personnel of the Anza-Borrego Desert State Park.

We are grateful to Charles A. McLaughlin for making the drawings and reading the manuscript critically; to Alice White and Edward D. Mitchell Jr. for preparation of the map and diagrams; and to G. Davidson Woodard for aid in stratigraphic interpretations.

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We wish to thank the following individuals and institutions for the loan of comparative material: E. Raymond Hall and Robert W. Wilson, University of Kansas Museum of Natural History (U.K.M.); William B. Davis, Department of Wildlife Management, Agricultural and Mechanical College of Texas (T.A.M.); C. Lewis Gazin and Charles Handley, United States National Museum (U.S.M.); Seth B. Benson, Museum of Vertebrate Zoology, University of California, Berkeley (M.V.Z.); W. Frank Blair, Department of Zoology, University of Texas (Z.U.T.); Bryan P. Glass, Department of Zoology, Oklahoma State University (O.S.U.); Donald F. Hoffmeister, Museum of Natural History, University of Illinois (U.I.M.); William D. Turnbull, Chicago Natural History Museum (C.N.M.); Rachel H. Nichols, American Museum of Natural History (A.M.N.), and Kenneth E. Stager and Charles A. McLaughlin, Los Angeles County Museum (L.A.M.).

The Genus *Geomys*

Pocket gophers are fossorial rodents that spend most of their time underground. They are, therefore, somewhat sedentary, and populations tend to be confined in a relatively small area. According to Wright (1940, "Sewell Wright Effect"), the inbreeding of populations in a small area results in a random fixation of characters that usually does not occur in populations of larger areas. This may account for the well-known intraspecific variability of pocket gophers and may explain why the various species are not easily distinguishable morphologically (see Durrant, 1953). Statistical techniques are necessary in the study of the taxonomy of these forms.

The genus *Geomys* is defined by the following characteristics of the skull (Merriam, 1895): the upper incisors are doubly grooved on the anterior faces, the smaller, shallower groove being situated medially to the larger, deeper one. P^4 in adult individuals lacks enamel on the posterior border of the biting surface. M_1 and M_2 lack enamel on the anterior borders of the biting surfaces.

All the teeth in *Geomys* are rootless and ever-growing. The occlusal surface of the grinding teeth is characterized by the presence of alternating bands of enamel and dentine. These "bands" are formed by the loss of enamel from the buccal, lingual, and, less often, from the anterior or posterior surfaces of the teeth.

The occurrence of *Geomys* in the Vallecito Creek Pleistocene is of interest, for the genus has never before been recorded from the fossil or Recent record in California. Extant and extinct species are known in eastern, central, and southwestern United States as far west as Lordsburg, New Mexico, and in northeastern Mexico (Fig. 1).

There are seven described, living species of *Geomys* (Fig. 1). Three of these (*G. cumberlandius*, *G. fontanelus*, and *G. colonus*) are represented by small, distinct populations found along the coast of the state of Georgia. The other four species (*G. bursarius*, *G. personatus*, *G. arenarius*, and

G. pinetis) are polytypic, containing two or more subspecies or geographic races.

Four extinct species have been described: *G. parvidens* (= *G. bursarius parvidens*) from the Conard Fissure Late Pleistocene of Arkansas; *G. tobinensis* from the Tobin Ranch local fauna Mid Pleistocene of Kansas; *G. quinni* from the Sand Draw local fauna Early Pleistocene of Nebraska; and *G. bisulcatus* from the ?Pliocene of Nebraska (Table 8).

Two extinct genera, closely related to *Geomys*, have been described: *Nerterogeomys* (*N. minor* and *N. persimilis*) from the Early to ?Mid Pleistocene of the San Pedro Valley of Arizona (Table 8); and *Pliogeomys* (*P. buisi*) from the Late Pliocene Buis Ranch local fauna of Oklahoma.



Fig. 1. Map showing the geographic distribution of the species of *Geomys* and of the genera, *Nerterogeomys* and *Zygozemys*. The encircled numbers refer to living species having a wide geographic distribution while the plain numbers refer to both living and extinct species having a limited geographic distribution.

- | | |
|----------------------------------|--|
| 1. <i>Geomys bursarius</i> | 9. <i>G. quinni</i> and <i>Nerterogeomys</i> |
| 2. <i>G. personatus</i> | 10. <i>G. tobinensis</i> |
| 3. <i>G. arenarius</i> | 11. <i>G. quinni</i> |
| 4. <i>G. pinetis</i> | 12. <i>Nerterogeomys</i> |
| 5. <i>G. fontanelus</i> | 13. <i>Nerterogeomys</i> |
| 6. <i>G. colonus</i> | 14. <i>G. garbanii</i> |
| 7. <i>G. cumberlandius</i> | 15. <i>Zygozemys</i> |
| 8. <i>G. bursarius parvidens</i> | |

Materials

All comparative materials used in this study are herein listed by species and subspecies name, together with region of collection, source institution (abbreviated as indicated under acknowledgments), and number of specimens.

Geomys bursarius (Shaw)

G. b. attwateri: Texas, U.S.M. 22, L.A.M. 9. *G. b. brazensis*: Texas, T.A.M. 10. *G. b. breviceps*: Louisiana, U.S.M. 25. *G. b. dutcheri*: Oklahoma, O.S.U. 28. *G. b. illinoensis*: Illinois, U.I.M. 25, L.A.M. 3. *G. b. industrius*: Kansas, U.K.M. 15. *G. b. jugossicularis*: Kansas, U.K.M. 11. *G. b. lutescens*: Kansas, U.K.M. 9. *G. b. major*: Kansas, U.K.M. 18; New Mexico, L.A.M. 5. *G. b. majusculus*: Kansas, U.K.M. 20. *G. b. pratincolus*: Texas, T.A.M. 10. *G. b. sagittalis*: Texas, T.A.M. 6.

G. personatus True

G. p. fallax: Texas, Z.U.T. 25, U.S.M. 1. *G. p. megapotamus*: Texas, Z.U.T. 25. *G. p. personatus*: Texas, L.A.M. 5.

G. arenarius Merriam

G. a. arenarius: Texas, M.V.Z. 15; New Mexico, L.A.M. 6. *G. a. brevirostris*: New Mexico, M.V.Z. 19, L.A.M. 5.

G. pinetis Rafinesque

G. p. austrinus: Florida, L.A.M. 1. *G. p. floridanus*: Florida, U.S.M. 14. *G. p. mobilensis*: Florida, L.A.M. 1.

Geomys bursarius (Shaw)

G. bursarius: Kansas, Cragin Quarry local fauna, Late Pleistocene (Hibbard 1960), U.K.M. 1 cranium. *G. b. parvidens*: Arkansas, Conard Fissure, Late Pleistocene (Brown 1908), A.M.N. 1 cranium, 18 mandibles, 4 palates.

Geomys quinni McGrew

G. quinni: Nebraska, Sand Draw local fauna, Early Pleistocene (McGrew 1944), C. N. M. 12 mandibles and other miscellaneous elements and fragments; Kansas, Rexroad Fauna, Early Pleistocene (Franzen 1947), U.K.M. 3 mandibles.

Geomys tobinensis Hibbard

G. tobinensis: Kansas, Tobin Fauna, Mid Pleistocene (Hibbard 1944), U.K.M. 1 mandible with $P_4 - M_2$; 1 P_4 .

Methods used in the study of variation

Two types of variants were studied. One type involves analysis of measurements of continuous variation, the other analysis of arbitrary categories of discontinuous variants, such as categories of shapes or degrees of expression of unmeasurable characters.

Measurements were made with dial calipers calibrated to 0.1 mm. All measurements were taken in exactly the same manner to reduce sampling error. In selecting measurements it was felt that the usual measurements of the neo-mammalogist as well as those of the students of fossil *Geomys* should be used in order to provide comparisons with living

members of the genus. Charles A. McLaughlin, Associate Curator of Mammals at the Los Angeles County Museum, who recently completed a manuscript on the taxonomy of certain groups of living *Geomys*, was consulted in the selection of these measurements.

The measurements of the cranium were taken as follows:

BASILAR LENGTH: from the posterior surface of the upper incisor at the alveolus to the ventral, medial notch of the foramen magnum.

LENGTH OF THE ALVEOLUS OF THE UPPER CHEEK-TOOTH ROW: from the anterior edge of the alveolus of P^1 to the posterior edge of the alveolus of M^3 .

LENGTH OF UPPER DIASTEMA: from the posterior surface of the upper incisor at its alveolus to the anterior edge of the alveolus of P^1 .

LEAST INTERORBITAL CONSTRICTION: self explanatory.

BREADTH OF ROSTRUM AT THE VENTRAL EDGE OF THE INFRAORBITAL CANALS: taken by placing the points of the calipers in each opening of the infraorbital canals and holding calipers perpendicular to the antero-posterior axis of the skull.

BREADTH OF ROSTRUM AT THE MAXILLARY-PREMAXILLARY SUTURE ON SIDE OF ROSTRUM: self explanatory.

LEAST DEPTH OF ROSTRUM: taken at the narrowest part of the rostrum by placing one point of the calipers on the arched premaxillary (ventrally) and the other point on the dorsal surface of the nasals.

PALATOFRONTAL DEPTH OF SKULL: from the ventral surface of the bony palate to the dorsal surface of the frontals.

The measurements of the mandible were taken as follows:

LENGTH OF MANDIBLE: from the posterior surface of a lower incisor at the alveolus to the posterior-most surface of the condyloid process.

LENGTH OF THE ALVEOLUS OF THE LOWER CHEEK-TOOTH ROW: as in the upper cheek-tooth row.

LENGTH OF LOWER DIASTEMA: as in the upper diastema.

DISTANCE FROM CONDYLOID TO ANGULAR PROCESS OF MANDIBLE: from the dorso-medial surface of the condyloid process to the ventro-lateral surface of the angular process.

TOOTH-ROW PROJECTION TO MENTAL FORAMEN: from the "ventral" surface of a straight edge layed on the biting surface of P_4 to the mental foramen. In each case the shortest distance between the mental foramen and the straight edge was estimated.

MENTAL FORAMEN TO POSTERIOR SURFACE OF M_2 : from the mental foramen to the mid-point on the posterior edge of M_2 .

The establishment of categories for "unmeasurable" characters is best done in the discussion of such categories.

Statistical analysis was made for each of the samples when such samples were sufficiently large to permit analysis. For each sample, the mean, standard deviation, standard error of the mean, coefficient of

variability, and Student's *t*-value (Simpson *et al*, 1960) of the 95 per cent confidence level, were obtained.

To test the significance of differences between the various samples, a modification of the Dice-Leraas (1936) method was chosen. In cases where it was deemed desirable to check further the degree of difference between two samples, a *t*-value was calculated and the limits indicated by it listed along with the mention of such comparisons in the text. The limits of the *t*-values generally accepted as indicating significant differences between two samples range between .05 and .001, which means that only 5.0 to 0.1 per cent of the time would a value fall outside of these limits (Simpson *et al*, 1960). For example, when the length of the lower cheek-tooth row in *G. garbanii* is compared with that in *G. p. megapotamus*, the calculated *t*-value is 2.570. Using the appropriate table, the *t*-value falls between 2.473 and 2.771 and would be expected to fall outside of these limits only 1 to 2 per cent of the time. The two samples, therefore, are probably significantly different to the .02 level of significance.

The specimens used in analyses were adults. The segregation of specimens into juveniles and adults was done somewhat subjectively and based on: (1) the degree of sutural fusion, especially between the basisphenoids and basioccipitals, and between the supraoccipitals and exoccipitals; (2) the degree of development of the sagittal crest or the extent to which the ridges which limit the dorsal extension of the temporal muscles approximate one another on the dorsal surface of the skull; (3) the presence or absence of enamel plates or the interruption of the enamel band around P^4 and P_4 ; (4) the relative size of the specimens within a given sample. This latter criterion is the least reliable, but nevertheless seems to serve well, and was necessarily used in dealing with fragmentary material.

*Geomys garbanii*³ new species

The *Geomys* from the Vallecito Creek fauna is distinct from all other species of the genus and, thus, is accorded a new name and described and discussed below.

HOLOTYPE: L.A.M. No. 3483; nearly complete cranium and associated mandibles.

TYPE LOCALITY: L.A.M. Vert. Paleo. loc. no. 1380. Vallecito Creek, Carrizo Mountain quadrangle, 1953. AMS sheet 2749 1, series V795, San Diego Co., California; grid coordinates 11,575,500 — 3,641,000.

FAUNA: Vallecito Creek.

AGE: Middle Pleistocene, Irvingtonian provincial age; also see Downs (1957); complete faunal report to be published.

FORMATION: Palm Springs (see Downs, *in* report of Continental Cenozoic Committee of the Society of Vertebrate Paleontology, *in press*).

REFERRED MATERIAL: (listed according to element, L.A.M. locality

³Named for Harley J. Garbani, the discoverer of the Vallecito Creek vertebrate fauna.

no., and catalog no.). Cranium and associated mandibles: loc. 1192, no. 3231; loc. 1314, no. 3480; cranium: loc. 1296, no. 3481; loc. 1314, no. 3525; posterior part of cranium with bullae and M^2 M^3 : loc. 1197, no. 3229; partial cranium and associated mandibles: loc. 1192, no. 3230; loc. 1316, no. 3511; loc. 1508 or 1509, no. 4185; loc. 1548, no. 4244; partial rostra: loc. 1114, no. 1553; loc. 1191, no. 3252; loc. 1192, nos. 3352, 3491; loc. 1249, no. 3354; loc. 1296, no. 3500; loc. 1314, no. 3526; loc. 1317, no. 4186; loc. 1318, no. 3518; loc. 1386, no. 4187; loc. 1518, no. 4199; palate with both rows of cheek-teeth: loc. 1246-3, no. 3384; loc. 1514, no. 4189; undersurface of rostrum: loc. 1325, no. 4190; interorbital area: loc. 1297, no. 3524; P^4 : loc. 1114, nos. 3404.1, 3404.2, 3404.3; M^3 : loc. 1297, no. 4191; mandibles: loc. 1113, nos. 1583, 3403; loc. 1114, nos. 1551, 1552, 1554; loc. 1191, nos. 3244, 3250; loc. 1192, nos. 3352, 3492; loc. 1197, no. 3228; loc. 1248, no. 3684; loc. 1250, no. 3347; loc. 1296, no. 3499; loc. 1297, nos. 3482, 3485, 3486, 3488, 3494, 3495, 3501, 3502, 3503, 3504, 3524; loc. 1299, no. 3487; loc. 1300, no. 3496; loc. 1308, no. 3484; loc. 1313, no. 3497; loc. 1314, no. 4192; loc. 1316, nos. 3508, 3509, 3510; loc. 1317, nos. 3514, 3515; loc. 1318, nos. 4193, 3516, 3517; loc. 1324, nos. 3519, 3520; loc. 1333, no. 3521; loc. 1336, no. 4194; loc. 1337, no. 3522; loc. 1448, no. 4198; loc. 1474, no. 4195; loc. 1500, no. 4196; loc. 1511, no. 4197; loc. 1518, no. 4188; loc. Vallecito Creek, no. 3523; partial pelvis and other doubtfully associated bones: loc. 1192, unnumbered.

DIAGNOSIS: Large, about the size of a large *Geomys bursarius* or *G. personatus*; rostrum deeper; tympanic bullae and opening of the external auditory meatus larger than in any other species.

DESCRIPTION OF THE HOLOTYPE: A skull (Fig. 16) and associated mandibles of a fully adult animal. Left zygomatic arch present and parallel to longitudinal axis; supraorbital ridges high, delimiting a trough-like depression between them; sagittal crest not quite formed, but dorsally placed ridges bounding the temporal muscle scar about 3 mm. apart; skull table flat and rostrum sloping ventro-anteriorly; nasals slightly flared anteriorly, nearly parallel-sided in the posterior one-third; external auditory meatus opening dorsally, posterior to zygomatic arch and measuring 2.6 mm. in inside diameter and 4.6 mm. in outside diameter; lambdoidal crest moderately developed; anterior surface of upper incisors posterior to anterior extension of nasals; rostrum, dorsally, approximately as broad as deep; cheek-tooth rows diverging posteriorly, and posterior extent of palate distinctly posterior to right and left M^3 ; tympanic bullae large, with inner margins diverging posteriorly to level of ventral notch of foramen magnum; tube-like structure enclosing auditory meatus extending dorso-anteriorly, terminating in a large external opening; coronoid, condyloid, and angular processes of the left mandible broken at their tips; a shallow pit present between coronoid process and capsular process of lower incisor root; valley absent between condyloid and capsular processes; mental

foramen anterior to P_4 and anterior to foremost extension of masseteric scar.

Detailed Description

Clearly a member of the genus *Geomys*: bisulcate upper incisors; enamel plate usually completely absent from posterior surface of P^4 and always absent from anterior surfaces of M_1 and M_2 in adults.

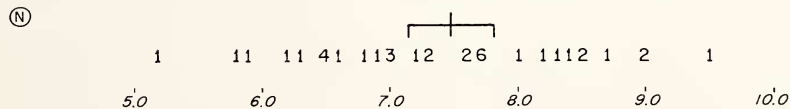
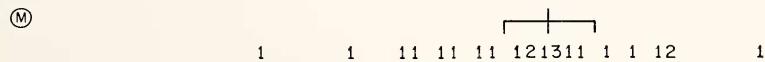
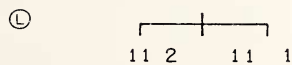
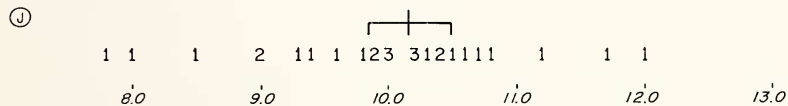
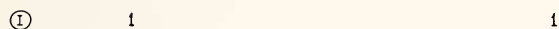
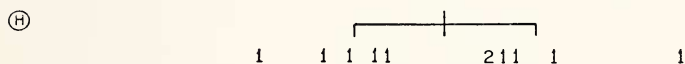
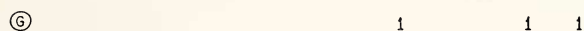
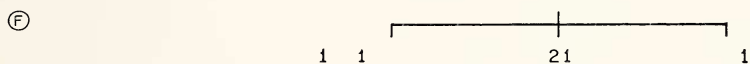
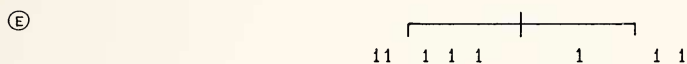
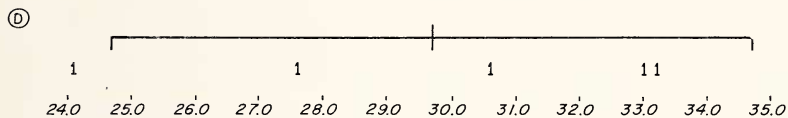
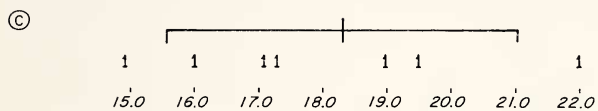
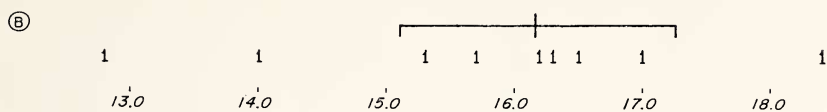
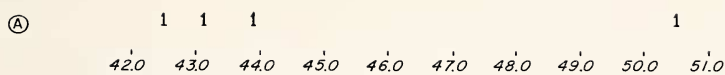
THE SKULL: Supraorbital ridges high and more developed than in other species, a depression in the frontal bone between them; tympanic bullae markedly inflated and larger than in any other species; external auditory meatus markedly larger than in any other species (see Fig. 13); length of basioccipital (although difficult to measure in adult specimens) seeming to exceed, in some specimens, the breadth of the rostrum at the maxillary-premaxillary junction, and to be less than this breadth in other specimens; zygomatic arches parallel to longitudinal axis of cranium; rostrum noticeably deeper, dorso-ventrally; upper incisors more recurved than in other species, and their anterior surfaces posterior to anterior extension of nasals; skull table flattened and rostrum sloping slightly ventrally and anteriorly; sides of nasal bones more or less straight, convergent and truncated posteriorly.

The relationship of the length of the basioccipital to the breadth of rostrum at the maxillary-premaxillary junctions is difficult to determine because the suture between the basioccipital and basisphenoid is frequently absent, but the basioccipital seems longer than the rostrum is wide in the holotype and the reverse in specimen no. 3231. This character has been used to distinguish *G. personatus* and *G. arenarius* on the one hand, from *G. bursarius* and *G. pinetis* on the other hand, without any "overlap" (Davis, 1940).

Table 1



Frequency distribution of the measurements of specimens of *G. garbanii* n. sp. All measurable specimens are included (in millimeters). The mean and confidence limits are plotted over each frequency distribution. No confidence limits were calculated for basilar length of skull, depth of rostrum, and the distance from condyloid to angular process. The encircled capital letters correspond to skull measurements as follows: A. basilar length of skull; B. length of upper diastema; C. palatofrontal depth of skull; D. length of mandible; E. length of upper cheek-tooth row; F. breadth of rostrum at the maxillary-premaxillary junction; G. depth of rostrum; H. length of lower cheek-tooth row; I. distance from condyloid to angular process; J. distance from mental foramen to posterior surface of M_2 ; K. least interorbital constriction; L. breadth of rostrum ventral to infra-orbital canals; M. length of lower diastema; N. lower tooth-row projection to mental foramen.



THE MANDIBLE: The position of the mental foramen varies considerably from a position ventral to P_4 , and the anterior extension of the masseteric scar to a position anterior to these structures. This variability does not seem to be correlated with stratigraphic position in the section, but is present when a series of specimens is collected at a given locality. The position of the mental foramen is, therefore, variable and of little or no taxonomic significance. The dentary foramen is variably placed with respect to the posterior end of the pit between M_3 and the ascending ramus, and may be oriented nearly at right angles with the medial border of the pit for insertion of the temporal muscle, or the angle may be as much as an estimated 135 degrees.

Table 2

Statistical data relating to fourteen measurements taken on specimens of *Geomys garbanii* n. sp. The capital letters refer to measurements as indicated in Fig. 2. The abbreviations are as follows: ar. m. = arithmetic mean; N = number of items in sample; st. e. m. = standard error of the mean; t = student's t -value of confidence limits; s = standard deviation; V = coefficient of variability.

	N	ar. m.	Min.	Max.	st. e. m.	t	V	s
A	4	45.0	42.5	50.5	2.37	6.561	9.1	.11
B	7	11.0	9.9	12.3	.393	.888	8.7	.962
C	8	16.2	14.0	18.4	.472	1.08	7.7	1.29
D	6	7.4	6.2	8.1	.320	.753	4.4	.717
E	6	5.6	5.0	6.2	.228	.512	8.8	.487
F	5	11.3	9.8	12.8	.534	1.33	9.4	1.07
G	3	10.9	10.1	11.5	—	—	—	—
H	6	18.3	14.9	22.0	1.16	2.72	14.1	2.59
I	5	29.7	24.1	33.2	2.02	4.99	13.6	4.03
J	10	10.4	9.0	12.3	.336	.724	9.7	1.01
K	21	8.3	7.1	9.9	.164	.334	8.8	.74
L	1	11.3	—	—	—	—	—	—
M	34	7.5	5.9	9.5	.159	.319	12.2	.916
N	25	10.2	8.5	12.0	.165	.334	8.0	.808

The diastema tends to be shorter in *G. garbanii* (see figs. 2-5 and table 2), when specimens of *G. garbanii* are compared with specimens of comparable size in any other species. No valley exists between the capsular process of the root of the lower incisor and the condyloid process. This character is as in the other species of *Geomys* and unlike *Pliogeomys* as shown by Hibbard (1954). Between M₃ and the ascending ramus there is a pit for insertion of the temporal muscle; the pit seems shallower than in most species of the genus. (continue on P. 18)

Table 3

Frequency in number and per cent of variations in expression of the postero-lateral fold of M³.

Species	Absent		Slight		Marked	
	N	%	N	%	N	%
<i>Geomys garbanii</i>	3	23.2	5	38.4	5	38.4
<i>G. bursarius</i>	114	75.6	34	22.5	3	1.9
<i>G. personatus</i>	34	62.0	18	32.5	3	5.5
<i>G. arenarius</i>	20	58.9	13	38.2	1	2.9
<i>G. pinetis</i>	6	42.8	7	50.0	1	7.2
<i>All Living Species Combined</i>	174	59.8	72	35.8	8	4.4

Table 4

Antero-posterior, outside diameter of the external opening of the auditory meatus in *G. garbanii* compared with two species that seem to have the largest such structures. For abbreviations see Table 2.

Name	N	ar. m.	Min.	Max.	st. e.m.	t	V	s
<i>Geomys arenarius brevirostris</i>	14	2.6	2.1	3.0	.083	.179	12.1	.312
<i>G. personatus megapotamus</i>	18	2.9	2.4	3.3	.058	.122	8.6	.246
<i>G. garbanii</i>	3	4.6	3.9	5.3	—	—	—	—

Table 5

Measurements of *Geomys bisulcatus* Marsh (1871) and *G. garbanii* (six numbered L.A. County Museum specimens). All measurements in millimeters.

	<i>G. bisulcatus</i>	<i>Geomys garbanii</i>					
		3483	3231	3481	3230	3525	3482
Transverse diameter of upper incisor	3.4	2.8	3.2		2.7		
Antero-posterior extent of upper incisor	4.2	3.5	3.3		3.3		
Depth of skull at the premaxillary suture	12.7	13.3	14.5	12.7			
Length of lower incisor on arc of curve	31.8	35.6	33.1		32.9		
Transverse diameter of apex of lower incisor	3.2	2.8	2.9		2.7		
Depth of lower jaw below first molar	11.9	10.4	11.3		10.9	11.9	8.6
Antero-posterior extent of P ₄ -M ₂	7.4	6.7	7.1		7.3	7.5	7.3

Table 6

The mean and other statistical data pertaining to the calculated incisor length in several kinds of pocket gophers. Abbreviations as in Table 2.

Name	N	ar. m.	Min.	Max.	st. e. m.	t	V	s
<i>Geomys bursarius majusculus</i>	17	35.6	32.7	39.0	.487	1.003	5.5	1.95
<i>G. personatus megapotaamus</i>	24	34.2	30.2	36.4	.426	.861	5.9	2.04
<i>G. arenarius brevirostris</i>	19	35.4	31.8	37.8	.538	1.101	6.4	2.28
<i>G. garbanii</i> *	3	38.5	32.0	42.2	—	—	—	—
<i>G. quinni</i>	1	44.2	—	—	—	—	—	—

*One immature specimen (measuring 32.2) has the same relative incisor length as in specimens of living species. The other two specimens are adults and have markedly longer incisors.

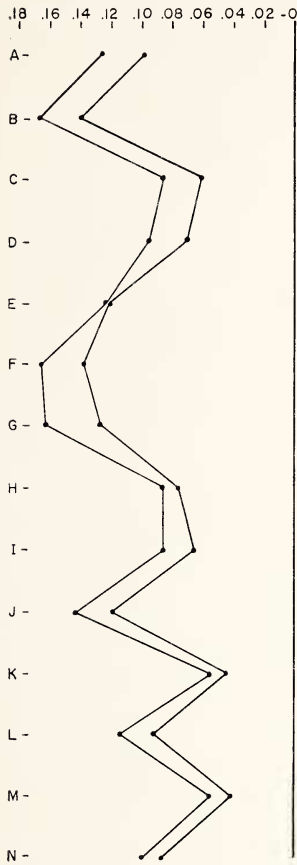


Fig. 2

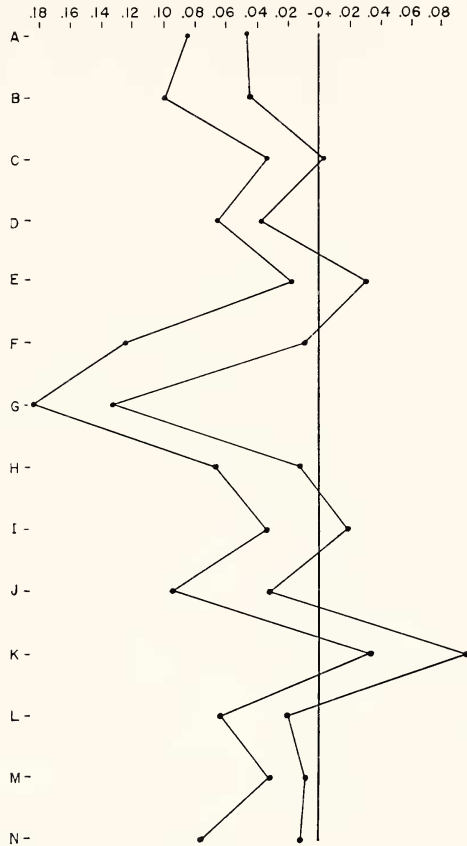


Fig. 3

Figs. 2-3. Ratio diagrams modified from Simpson *et al* (1960), comparing dimensions of the skull in *Geomys arenarius* (Fig. 2) and *Geomys personatus* (Fig. 3) with those in *G. garbanii*. The logs of the means of the dimensions in the latter species are assumed to be zero. The differences between the log of the mean in *G. garbanii* (standard) and species being compared are plotted to the positive (+) or negative (-) sides of the zero line. For each measurement the largest and the smallest means of the species being compared are used. The capital letters to the left of the diagrams in figures 2-5 refer to skull dimensions as follows: A. basilar length of skull; B. length of upper cheek-tooth row; C. length of upper diastema; D. least interorbital constriction; E. breadth of rostrum ventral to the infraorbital canals; F. breadth of rostrum at the maxillary-premaxillary junction; G. depth of rostrum; H. palato-frontal depth of skull; I. length of mandible; J. length of lower cheek-tooth row; K. length of lower diastema; L. distance from condyloid to angular process; M. lower tooth-row projection to mental foramen; N. mental foramen to posterior surface of M_2 .

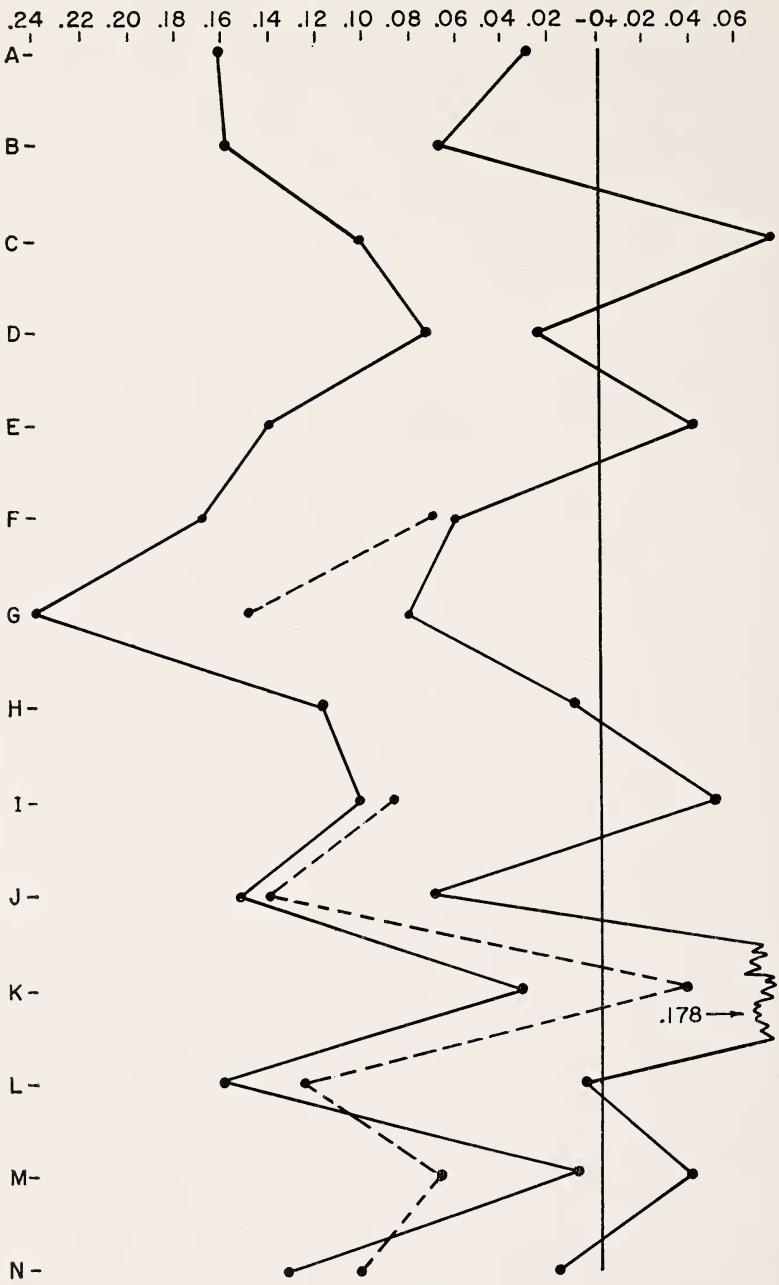


Fig. 4. Ratio diagrams modified from Simpson *et al* (1960), comparing dimensions of the skull in *Geomys bursarius* and *G. b. parvidens* (broken line) with those in *G. garbanii*. For additional details see Fig. 2.

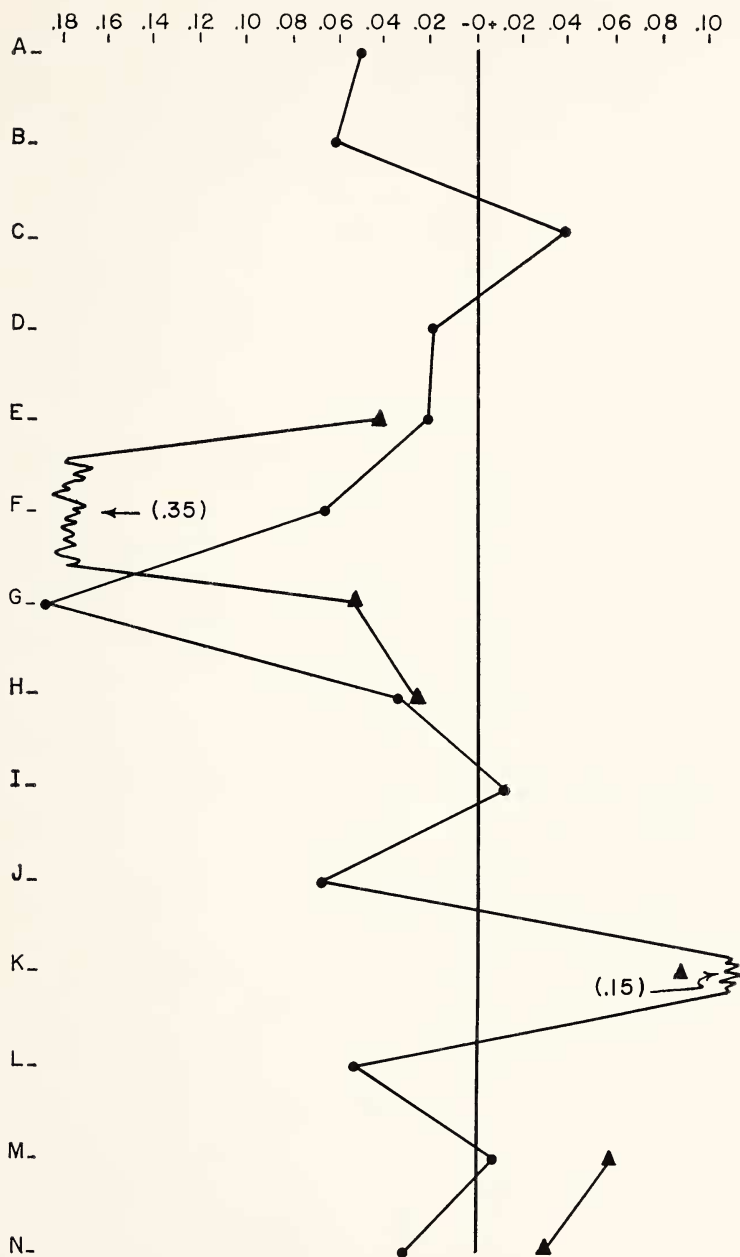
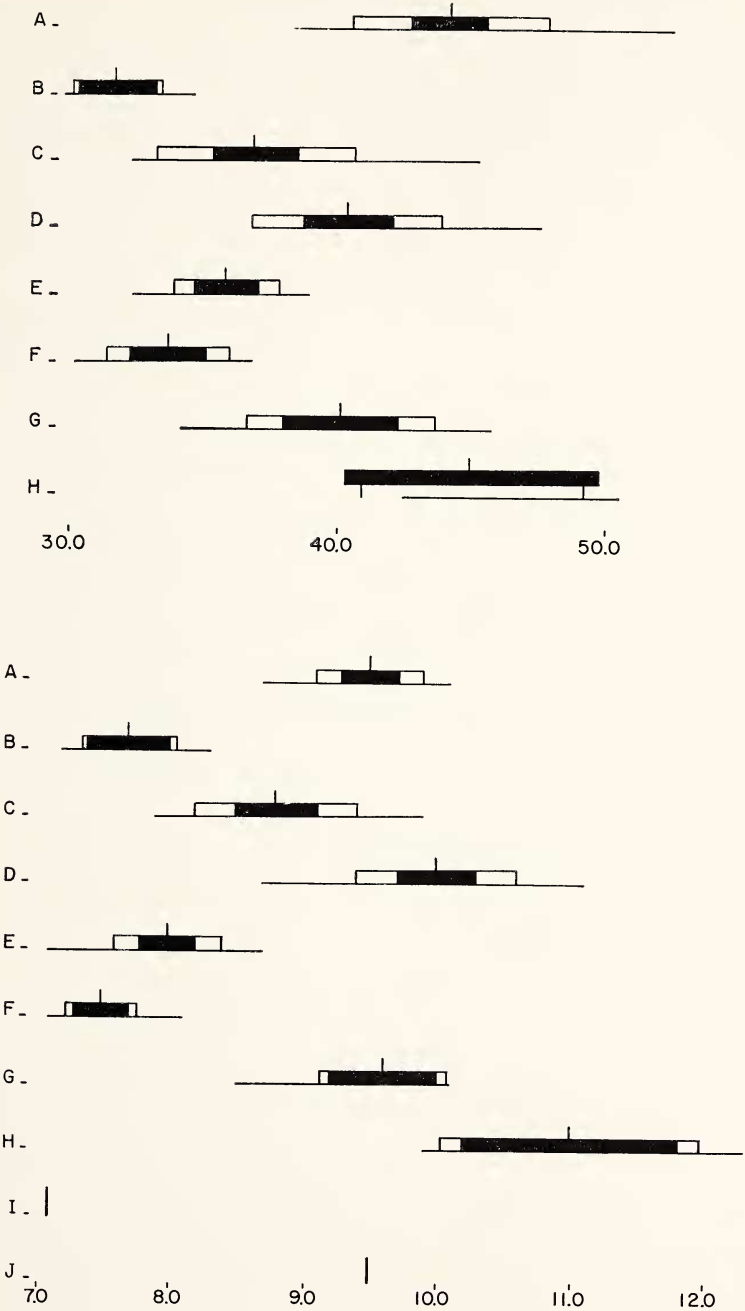


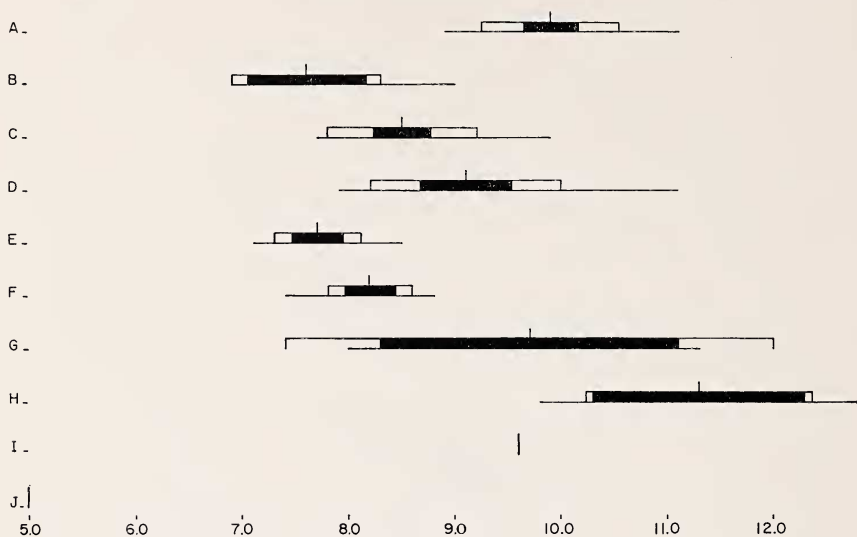
Fig. 5. Ratio diagram modified from Simpson *et al* (1960), comparing dimensions of the skull in *Geomys pinetis* (dots) and *G. quinni* (triangles) with those in *G. garbanii*. For additional details see Figs. 2 and 3.

DENTITION: The upper incisors in *G. garbanii* are bisulcate as in all *Geomys*. As in *G. quinni*, the upper incisors are more procumbent (re-curved) than in any other species (W. D. Turnbull examined this character for us on the type specimen of *G. quinni*). The anterior surfaces of these incisors are posterior to the anterior extension of the nasals in both latter species (Figs. 16 and 17). No other species of geomyid has this character (Wilson 1949). The upper and lower series of grinding teeth are rootless and evergrowing. Reentrants on P^4 and P_4 are nearly parallel-sided, forming right angles with their innermost boundaries. In this regard *G. garbanii* is like all other species except *G. quinni* wherein sides of reentrants diverge (Franzen 1947). This latter condition is found in P^4 and P_4 of immature specimens of all species and may represent an embryonic character which persists in adults only of *G. quinni*. Enamel patterns of P^4 and P_4 are interrupted by bands of dentine as in living species. The enamel forms a continuous layer completely surrounding the dentine of the occlusal surface in immature specimens of all species. On the sides of such teeth are inverted "V's" (see Fig. 15) of dentine (Hibbard, 1954) which, with additional wear of the occlusal surface would cause the apex of the "V's" to reach the occlusal surface and thus interrupt the ringing bands of enamel. We were unable accurately to determine by measurement how far down the side of the unworn P^4 and P_4 the apices of the "V's" of dentine may be found. In *G. garbanii*, *G. tobinensis*, and *Nerterogeomys* the interruption of the enamel patterns of P^4 and P_4 , if at all, seems to occur later in the life history of individuals than in the other species. One specimen of *G. garbanii* (No. 1553), is the cranium of a fully adult individual and has enamel on the lingual side of the posterior edge of P^4 (Fig. 14). This characteristic was noted by Hibbard (1954) in *G. tobinensis*, and Merriam (1895) noted it in *Zygogeomys*, a genus now known to occur in a restricted area in Mexico. Most adult specimens of *G. garbanii* have a lateral (buccal) reentrant fold on M^3 (Fig. 14), and this occurs more frequently than in adults of the several living species (Table 3).

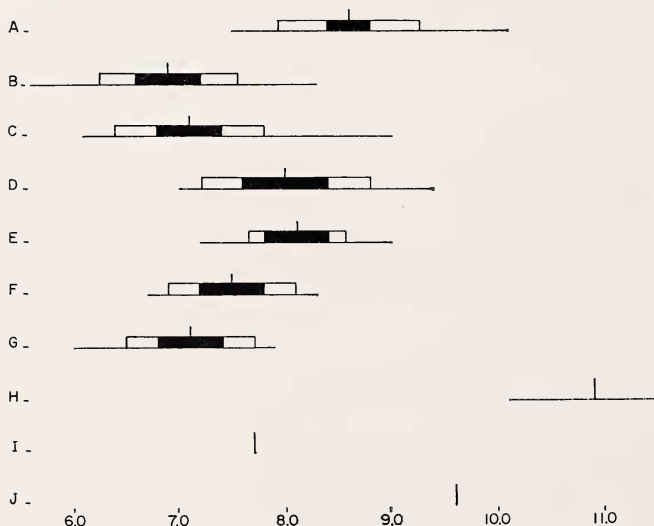
Figs. 6, 7. Bar diagrams modified from Dice and Leraas (1936) showing variations in skulls of several kinds of pocket gophers. In each of the diagrams, the vertical line represents the mean of the sample, the darkened area two standard errors of the mean, the white areas a standard deviation on either side of the mean, and the line at the bottom the observed range. The capital letters on the left correspond to samples of the respective taxa (size of sample in parentheses). Fig. 6 (above). Variation in basilar length of skull. [Only the largest and smallest (dimension of specimen) subspecies of *G. bursarius* are used.] A. *Geomys bursarius illinoensis* (24); B. *G. b. pratincolus* (8); C. *G. personatus fallax* (25); D. *G. p. megapotamus* (19); E. *G. arenarius arenarius* (13); F. *G. a. brevirostris* (14); G. *G. pinetis floridanus* (13); H. *G. garbanii* (4). Fig. 7 (below). Variation in length of upper cheek-tooth row. A. *Geomys bursarius illinoensis* (24); B. *G. b. lutescens* (8); C. *G. personatus fallax* (25); D. *G. p. megapotamus* (19); E. *G. arenarius arenarius* (13); F. *G. a. brevirostris* (14); G. *G. pinetis floridanus* (13); H. *G. garbanii* (7); I. *G. bursarius parvidens* (1); J. *G. quinni* (1).







Figs. 8-9. Bar diagrams modified from Dice and Leraas (1936) showing variation in rostrum in several kinds of pocket gophers. The capital letters on the left of the bar diagrams correspond to samples of the respective taxa (size of sample in parentheses): Fig. 8 (above). Variation in breadth of rostrum at the maxillary-premaxillary junction. A. *Geomys bursarius illinoensis* (24); B. *G. b. pratincolus* (8); C. *G. personatus fallax* (25); D. *G. p. megapotamus* (19); E. *G. arenarius arenarius* (13); F. *G. a. brevirostris* (14); G. *G. pinetis floridanus* (13); H. *G. garbanii* (5); I. *G. b. parvidens* (1); J. *G. quinni* (1). Fig. 9 (below). Variation in the depth of rostrum. A. *Geomys bursarius majusculus* (15); B. *G. b. attwateri* (22); C. *G. personatus fallax* (25); D. *G. p. megapotamus* (18); E. *G. arenarius arenarius* (13); F. *G. a. brevirostris* (14); G. *G. pinetis floridanus* (13); H. *G. garbanii* (3); I. *G. b. parvidens* (1); J. *G. quinni* (1). For additional details see Fig. 6.



Comparisons with other species

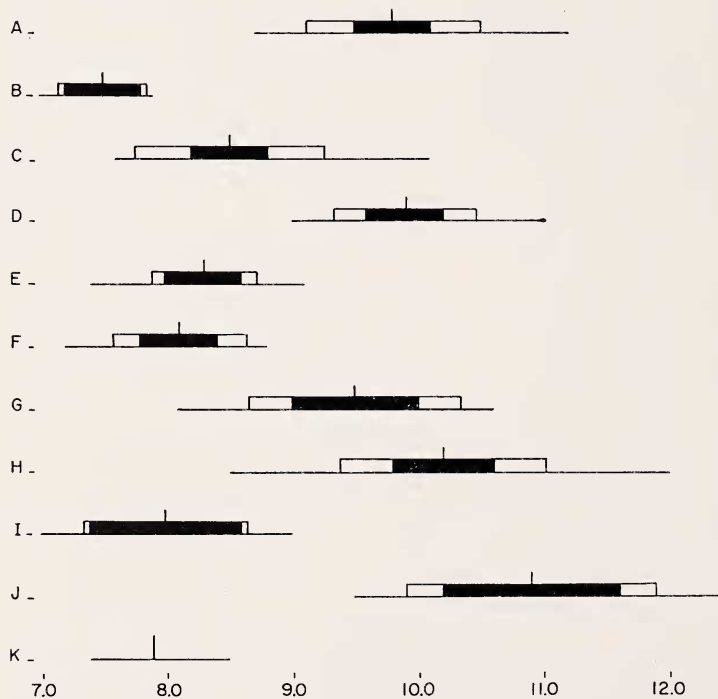
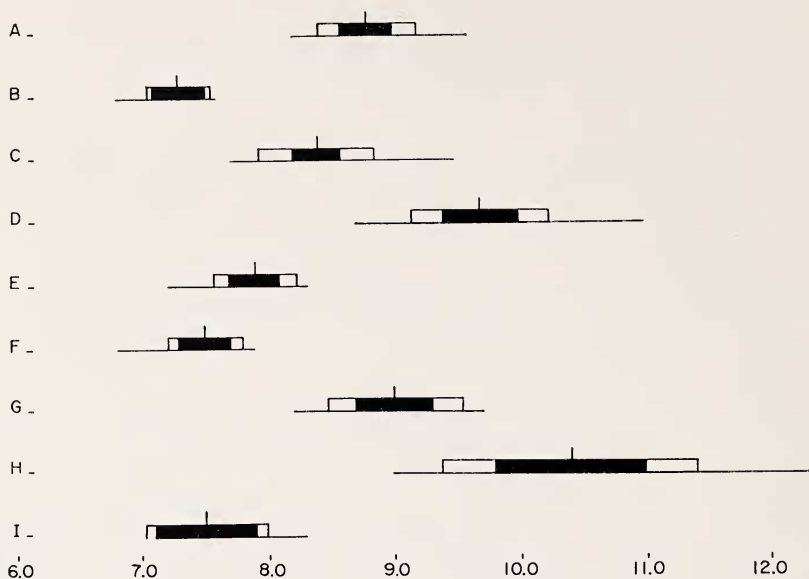
In the following paragraphs the species of the genus are compared to *Geomys garbanii*. A summary of these comparisons may be seen in Table 7 (p. 31).

Geomys bursarius (Shaw). *G. bursarius* differs from *G. garbanii* in: shorter cheek-tooth series; narrower rostrum at the maxillary-premaxillary junction; shallower rostrum; shorter distance from mental foramen to posterior surface of M_2 (except in *G. b. illinoensis* in which this distance is the same as that in *G. garbanii*); smaller tympanic bullae; smaller opening of the external auditory meatus; smaller in size of skull. The skull is larger in *G. garbanii* than in any subspecies except *G. b. illinoensis* and *G. b. majusculus*.

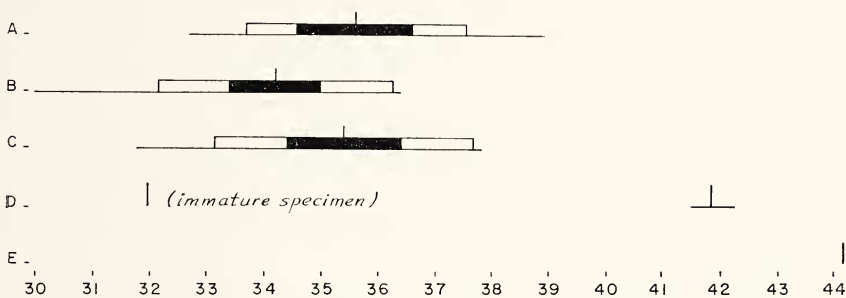
G. parvidens (Brown). In Brown's (1908) description of this species from the Conard Fissure Pleistocene he stated that it has a cheek-tooth row shorter than in any other species of the genus. However, when measurements of specimens of *G. parvidens* are compared statistically with measurements of the living species listed herein, no difference can be seen between *G. b. brazensis* and *G. b. sagittalis* (both are races of *G. bursarius* which are small in size) on the one hand, and of *G. parvidens* on the other. When the length of the lower cheek-tooth series of *G. parvidens* and *G. b. brazensis* are compared, the t-values fall within the .6 to .7 levels of significance (Fig. 4). Thus the measures and/or qualitative characters of *G. parvidens* do not differ significantly from those well within the range of variation of the subspecies of *G. bursarius*. We feel that *G. parvidens* should be given subspecific rank under *G. bursarius* as *Geomys bursarius parvidens*, for the following reasons: (1) the lack of morphologic difference between *G. parvidens* and *G. bursarius*, (2) the late geologic age (Late Pleistocene, Hibbard 1958) of the fauna from the Conard Fissure, and (3) the proximity of the Conard Fissure to the present geographic range of *G. bursarius* (see distribution map). It should be pointed out that the use of this trinomial does not imply to us any chronological or biological significance, and is retained only for the sake of convenience of reference.

G. personatus (True). *G. personatus* differs from *G. garbanii* in: shorter cheek-tooth series (statistical comparison reveals the limits of the t-values to fall between .01 and .001 level of significance in upper dentition and between .05 and .02 in lower dentition); shallower rostrum (t-values fall within a level of significance smaller than .001); narrower rostrum at the maxillary-premaxillary junction, except when senile specimens are compared with one another; smaller tympanic bullae; smaller opening of external auditory meatus (Figs. 3 and 13).

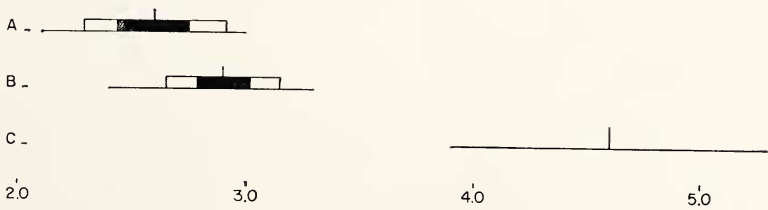
The cheek-tooth series in *G. garbanii* is longer than in any subspecies studied except for five senile specimens of *G. p. personatus* from Mustang



Figs. 10-11. Bar diagrams modified from Dice and Leraas (1936) showing variation in several kinds of pocket gophers. The capital letters on the left of the bar diagrams correspond to samples of the respective taxa (size of sample in parentheses): Fig. 10 (above). Variation in length of lower cheek-tooth rows. A. *Geomys bursarius illinoensis* (24); B. *G. b. pratincolus* (8); C. *G. personatus fallax* (25); D. *G. p. megapotamus* (19); E. *G. arenarius arenarius* (13); F. *G. a. brevirostris* (14); G. *G. pinetis floridanus* (13); H. *G. garbanii* (10); I. *G. b. parvidens* (5). Fig. 11 (below). Variation in the distance from mental foramen to the posterior surface of M₂. A. *Geomys bursarius illinoensis* (24); B. *G. b. pratincolus* (8); C. *G. personatus fallax* (25); D. *G. p. megapotamus* (16); E. *G. arenarius arenarius* (13); F. *G. a. brevirostris* (14); G. *G. pinetis floridanus* (13); H. *G. garbanii* (25); I. *G. b. parvidens* (6); J. *G. quinni* (8); K. *Nerterogeomys* (3). For additional details see Fig. 6.



Figs. 12-13. Bar diagrams modified from Dice and Leraas (1936) showing variations in several kinds of pocket gophers. The capital letters on the left of the bar diagrams correspond to samples of the respective taxa (size of sample in parentheses): Fig. 12 (above). Variation in the length of incisor (corrected, using the mean palato-frontal depth of skull in *G. b. majusculus* as a correction factor). A. *Geomys bursarius majusculus* (17); B. *G. personatus megapotamus* (24); C. *G. arenarius brevirostris* (19); D. *G. garbanii* (3); E. *G. quinni* (1). Fig. 13. Variation in outside diameter of the external auditory meatus. A. *Geomys arenarius brevirostris* (19); B. *G. personatus megapotamus* (18); C. *G. garbanii* (3). For additional details see Fig. 6.



Island, Texas, that should not be used in comparisons. Specimen No. 3480 of *G. garbanii* is of the same age and size as these Texas specimens, but is distinctly different except in length of cheek-tooth series. Thus, the length of the cheek-tooth series seems to reach its fullest development in younger specimens in *G. garbanii* than in living species.

G. arenarius (Merriam). *G. arenarius* differs from *G. garbanii* in: smaller tympanic bullae; smaller external opening of auditory meatus; presence of a "knob" on the zygomatic arch (this knob is absent from the only skull of *G. garbanii* having a complete zygomatic arch, see Figs. 13 and 16). The "knob" is used to distinguish *G. arenarius* from all other species (Davis, 1940).

G. pinetis Rafinesque (*G. p. floridanus* [Audubon and Bachman], the only subspecies of the species used in statistical analysis). *G. pinetis* differs from *G. garbanii* in: shorter cheek-tooth series (t-value falls within a level of significance smaller than .001); shallower rostrum; longer lower diastema; smaller tympanic bullae; smaller external auditory meatus; presence of nasals with consistent "hour-glass" shape in dorsal aspect (Figs. 7, 10, and 13).

G. quinni (McGrew). *G. quinni* differs from *G. garbanii* in: shorter cheek-tooth series; shallower rostrum (only one measurement is available for *G. quinni*); longer, lower diastema; markedly narrower rostrum at maxillary-premaxillary junction; divergent reentrant folds on P^1 and P_4 (Figs. 5, 7, 9, and 10).

G. tobinensis (Hibbard). *G. tobinensis* differs from *G. garbanii* in being smaller in all measured characters. In *G. garbanii* the pit between M_3 and the ascending ramus is well formed and ranges in estimated depth from shallow to moderately deep, while the pit in *G. tobinensis* is shallow.

The position of the dentary foramen with regard to the pit that receives the insertion of the temporal muscle varies from a position immediately above the posterior border of the pit to a position well posterior in *G. garbanii*. Relying on Hibbard's (1956, p. 183) description of three specimens of *G. tobinensis* (only one of which has been examined here), it would seem that *G. garbanii* may be more variable than *G. tobinensis* with regard to the position of the dentary foramen.

The interruption of the border of enamel on the biting surface of P_4 occurs later, ontogenetically, in *G. tobinensis* than in *G. garbanii*, making the latter intermediate, in this character, between *G. tobinensis* and the living species.

G. bisulcatus (Marsh). This species is known from two specimens (cotypes) which are in the collections of the Yale Peabody Museum. We were unable to see these specimens and have used Marsh's (1871) original description in making comparisons. The measurements taken by Marsh (op. cit.) were in lines, and these were translated into millimeters as seen in Table 5. The antero-posterior extent and width of the upper incisors

seem to be much greater in *G. bisulcatus* than in *G. garbanii*. The qualitative, descriptive characters of *G. bisulcatus* (of Marsh) are too variable to be used in comparisons.

Nerterogeomys (Gazin). In Gazin's (1942) description of this genus from the Early to Mid Pleistocene of the San Pedro Valley, Arizona, he listed the following generic characters: enamel present on the posterior wall of P^4 ; narrow anterior columns in P^4 and P_4 (as in the genus *Thomomys*); double-grooved upper incisors (as in *Geomys*); mental foramen below anterior extremity of masseteric scar; and rostrum more deeply depressed with respect to the plane of the cheek-teeth.

The variability in position of the mental foramen with respect to the anterior extent of the masseteric scar, as well as variability in the presence or absence of enamel on the posterior wall of P^4 in *G. garbanii*, suggests the possibility that *Nerterogeomys*, like *Parageomys* (Hibbard), might be considered a subgenus of the genus *Geomys*. This has been suggested by Hibbard (1954, 1956, and in personal communication). However, we feel that additional specimens of *Nerterogeomys* would be necessary if we were to attempt to make any taxonomic changes at this time.

Remarks concerning evolutionary relationships

The following characters of *Geomys* are tentatively thought to be primitive because they are absent, or at least not expressed in the same way, in Recent species, but apparently occur in all the extinct species.

1. Presence of a lateral groove (reentrant) on M^3 .
2. Interruption of the enamel pattern of P^4 and P_4 in the process of natural wear.

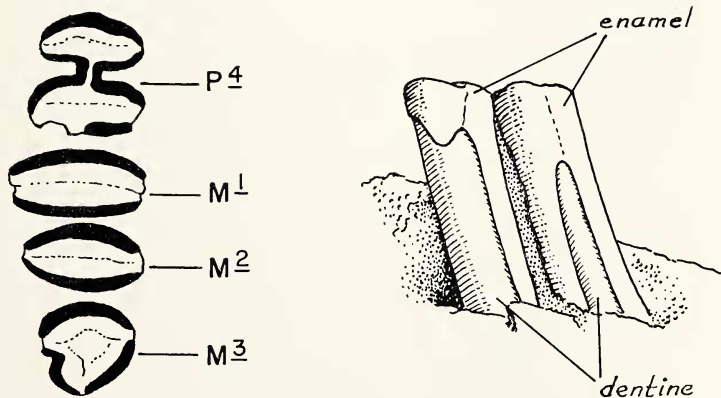


Fig. 14 (left). *Geomys garbanii* n. sp., no. 1114/1553. Occlusal view of upper right cheek-teeth.

Fig. 15 (right). *Geomys garbanii* n. sp., no. 1192/3353. Left medial view of P^4 .

3. Presence of an "open" reentrant on P^4 and P_4 (in adult specimens of *G. quinni* and juveniles of other species).
4. Relatively greater depth of rostrum.
5. Greater recurvation of the incisors and the consequent placing of the anterior face of the incisors posterior to the foremost extension of the nasals.
6. Enlarged tympanic bullae.

Using these "primitive" characters as a basis, it becomes possible to describe certain evolutionary trends within one branch of the geomyid rodents. The trends in each of the above characters are discussed in the order in which they are listed. Consult Table 8 for stratigraphic range of each species (p. 32).

THE LATERAL GROOVE ON M^3 : Merriam (1895: 80-83) described M^3 in the living pocket gophers, except in *Thomomys*, as being "... strengthened by three vertical bands of enamel, alternating with three interspaces filled with cement." Often the outer (lateral) or buccal enamel plate in living juvenal and adult *Geomys* and related genera, *Zygoeomys*, *Orthogeomys*, *Heterogeomys*, *Macrogeomys*, *Pappogeomys*, and *Cratogeomys*, is grooved (Fig. 14). The frequency of the presence of the groove in living *Geomys* can be seen in Table 3. Comparing the frequencies of the lateral groove on M^3 in adult *G. garbanii* with those in adults of extant species, it can be seen that the groove occurs more frequently in the extinct forms. The figured specimen (McGrew 1941) of *G. quinni* also seems to have this groove. It is suggested that the farther back in the fossil record one goes the longer (ontogenetically) the groove remains visible on the occlusal surface of the M^3 .

INTERRUPTION OF THE ENAMEL PATTERN OF P^4 AND P_4 IN THE PROCESS OF NATURAL WEAR: There is a delay in interruption of the enamel pattern of P^4 and P_4 in *G. garbanii* and *G. tobinensis*, as noted above. The pattern is not interrupted in any known specimen of *Nerterogeomys*, a genus which existed earlier in time than either of the two species mentioned above, if the Benson fauna can be thought of as Blancan in age. This variation from no interruption to delayed interruption to early interruption of enamel pattern indicates a trend similar to that seen for the lateral groove on M^3 . The farther back in the fossil record one goes the greater the delay (ontogenetically) in the interruption of the enamel pattern of P^4 and P_4 . All known specimens of *Zygoeomys*, a genus closely related to *Geomys*, have enamel on part of the posterior surface (buccal side) of P^4 , thus indicating delay in pattern interruption of P^4 . The figured specimens in Merriam (1895) and in Hall and Kelson (1959) seem to indicate a similarity of *Zygoeomys* to *G. garbanii* in other respects, and one is led to consider *Zygoeomys* a relict species living in a limited area in Mexico. As such, it would merit especial study.

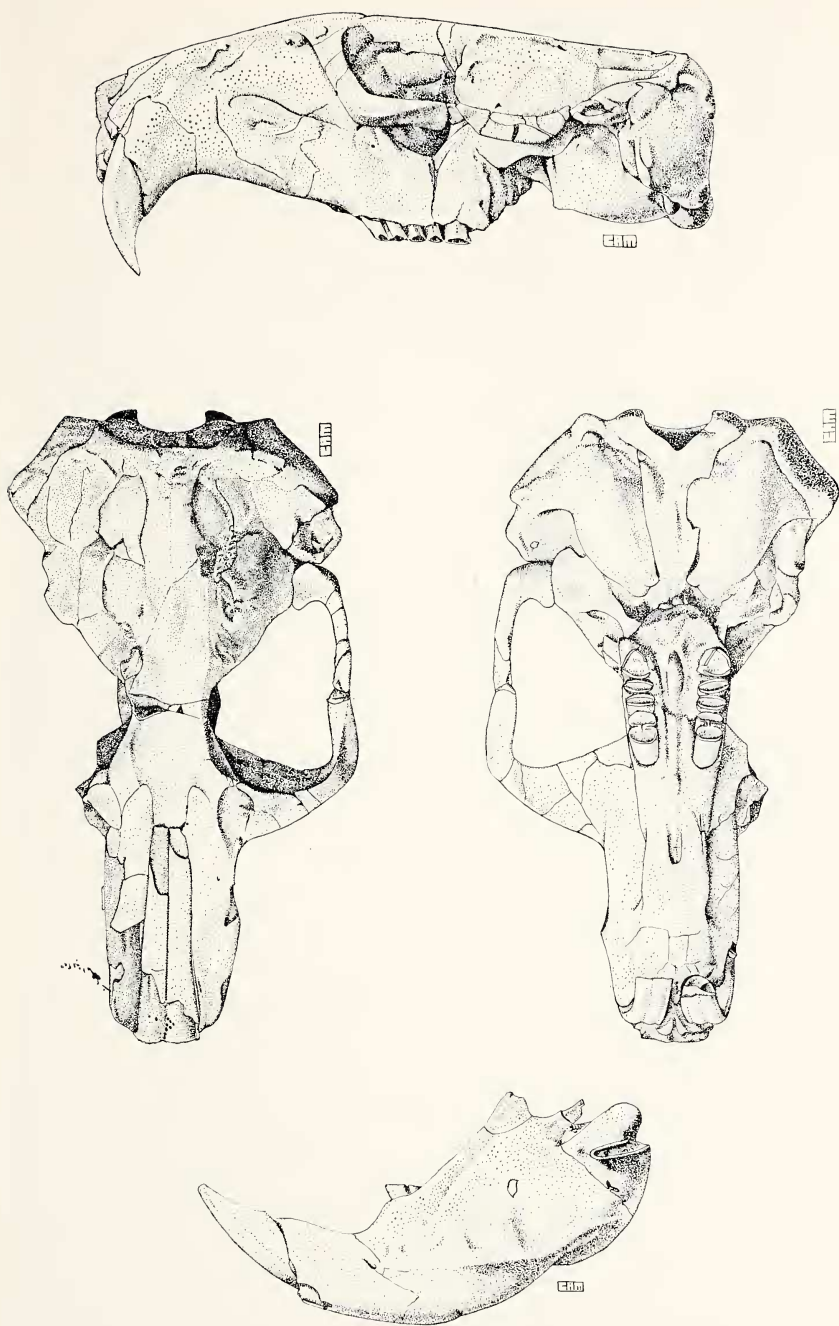


Fig. 16. *Geomys garbanii* n. sp., no. 1380/3483 (holotype): Lateral, dorsal and ventral views of skull (above); Left lateral view of mandible (below). All views $\times 1.6$.

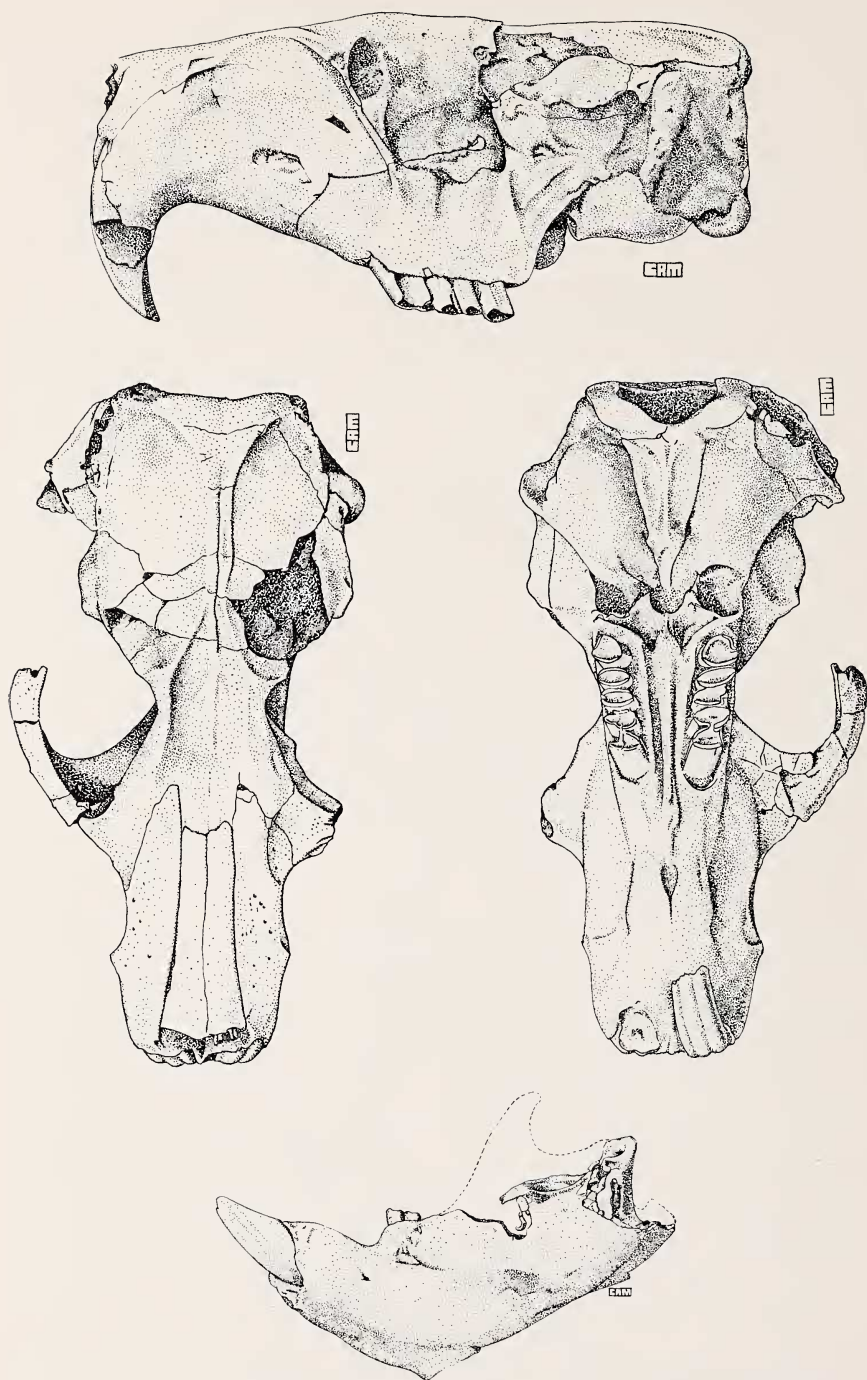


Fig. 17. *Geomys garbanii* n. sp. no. 1192/3231: Lateral, dorsal and ventral views of skull (above); Left lateral view of mandible (below). All views $\times 1.6$.

THE "OPEN" REENTRANT FOLD ON THE P^4 AND P_4 : The P^4 and P_4 in juvenal and adult specimens of *G. quinni* have divergent ("open") reentrants. This characteristic is lost early in the life history of specimens of living species (including *G. b. parvidens*) and is present in progressively older individuals of fossil species the farther one goes back in time.

RELATIVELY GREATER DEPTH OF ROSTRUM: In *G. garbanii* and *G. quinni* (the only extinct species in which the rostrum is known), the rostrum is distinctly deeper than in living species. It is possible that the deep rostrum is a primitive character, showing relationship to a similar type rostrum in the Heteromyidae.

OPISTHODONTY, OR THE GREATER RECURVATION OF THE UPPER INCISORS: In distinguishing the geomyids from the heteromyids, Wilson (1949: 116) noted, among other characteristics, that the nasals "... terminate behind rather than in front of the superior incisors . . ." This same idea can be restated as follows: In geomyids the teeth are proodont or orthodont, (projecting beyond the nasals and tip of incisors or with the nasals projecting anteriorly) while in the heteromyids they are opisthodont (tip of the incisor projecting posteriorly). These relationships must be observed from a lateral view with the dorsal surface of the nasals held in a horizontal position (see Figs. 16 and 17).

Landry (1957: 234) states, "... change from relatively straight incisors to more procumbent incisors is brought about principally by increase in the radius of curvature of the incisor, while change from straight incisors to strongly recurved incisors is brought about principally by increase in length of the incisor." The incisor lengths in one sample of each of the following species was determined: *G. bursarius majusculus*, *G. personatus megapotamus*, and *G. arenarius brevirostris*. These calculated data were used for comparisons with *G. garbanii* (see Table 6). In making the comparisons all such calculated lengths of incisors were "corrected" by using the mean of the palato-frontal depth of skull in *G. b. majusculus* as the standard to eliminate variations due to differences in size (see Landry). This technique seems to provide a means of measuring proodonty, orthodonty, and opisthodonty in rodents. *G. garbanii* and *G. quinni* (holotype examined for us by W. D. Turnbull) are the only species of extinct *Geomys* in which the rostrum is known, and in both, the adults are opisthodont. Taking into account the stratigraphic position of the two species, it is possible to interpret this to mean that opisthodonty is a primitive condition showing relationship to an heteromyid ancestor.

Both immature and adult specimens were used in obtaining the calculated lengths of incisors shown in figure 12. It can be seen that all immature and adult specimens of living *Geomys* (which were analyzed) are orthodont, while only the immature specimens of *G. garbanii* are orthodont. This comparison points to an evolutionary trend from opisthodont to orthodont in adult *Geomys*. This trend seems to indicate a reversal

of the ontogenetic relationships noted in the above discussions of P^4 and P_4 and M^3 .

ENLARGED TYMPANIC BULLAE: *G. garbanii* is the only extinct species of the genus in which the tympanic bullae are recorded. The fact that the bullae are somewhat larger in the fossil may again represent a primitive condition reminiscent of the condition in the heteromyids.

Morphologic stratigraphic relationship

The Vallecito Creek fauna has been collected, for the most part, throughout at least 2500 feet of the upper part of the Palm Spring formation, and *G. garbanii* has been collected at most horizons in the section. Comparisons of *G. garbanii* specimens from low in the section with those from higher in the section reveal no significant differences. Possibly the sediments were deposited in a relatively short period of time. This point will be discussed at a later time when an analysis of the entire fauna is made.

Comments on variation in *Geomys*

When measured skeletal and dental characters of the species (extant or extinct) are compared statistically with those of another species, the observed ranges of the two samples usually overlap (Figs. 6-11). Kennerly (1958 and 1959) found that although *Geomys bursarius* can be distinguished from *G. personatus* on the basis of external (non-skeletal) features and on ecological characteristics, the two species cannot easily be distinguished from one another on the basis of measured skeletal characters. We feel that the reason for this difficulty in attempting to distinguish morphologically between species lies in the high degree of intraspecific variability in local populations, races, and species. Variation within the living species of *Geomys* is great, especially within the species *G. bursarius* and *G. personatus* (Figs. 3 and 4).

McGrew (1944) used 8 specimens from each of the living species of *Geomys* for comparison when describing *G. quinni*, selecting only specimens of comparable size. His results, especially those shown in his ratio

Table 7

Summary of measured characters in *Geomys* species compared with *G. garbanii*. Where measurements are not shown to be equal, the + and - signs indicate that a structure is smaller or larger than in *G. garbanii* and that this difference is *significant* according to the standards employed in Dice Leraas (1936). The comparisons as shown for depth of rostrum and distance from condyloid to angular process are based only on means, since the number of these measurements in *G. garbanii* is too small for meaningful statistical analysis. The asterisks indicate a sample too small for meaningful statistical analysis.



NAME

NAME	Basilar length of skull	Length of upper tooth-row	Length of upper diastema	Least interorbital constriction	Breadth of rostrum ventral to infraorbital canal	Breadth of rostrum at maxillary-premaxillary juncture	Depth of rostrum	Palato-frontal depth of skull	Length of mandible	Length of lower tooth-row	Length of lower diastema	Condyloid to angular process	Mental foramen to tooth-row projection	Mental forament to posterior surfce of M ²
<i>Geomys bursarius attwateri</i>											+		+	
<i>G. b. brazensis</i>											+			
<i>G. b. breviceps</i>														
<i>G. b. dutcheri</i>														
<i>G. b. illinoensis</i>														
<i>G. b. indutrius</i>														
* <i>G. b. jugossicularis</i>														
<i>G. b. lutescens</i>														
* <i>G. b. major</i>			+											
<i>G. b. majusculus</i>														
<i>G. b. pratincolus</i>														
* <i>G. b. sagittalis</i>														
<i>G. personatus fallax</i>														
<i>G. p. megapotamus</i>														
<i>G. arenarius arenarius</i>														
<i>G. a. brevirostris</i>														
<i>G. pinetis floridanus</i>														
<i>G. b. parvidens</i>														
<i>G. quinni</i>														

diagram (op. cit., Fig. 17), are not substantiated in the larger sampling of the various species included in our comparisons.

Paleoecological inferences

Although a complete analysis of the Vallecito Creek fauna has not been made, the presence in the fauna of a few pertinent genera should be listed herein as being associated with *Geomys*.

The presence of *Sigmodon*, *Reithrodontomys*, *?Stegomastodon*, *Equus* (*?Plesippus*), and *?Lepus* may indicate a grasslands association and a moderate precipitation. *G. bursarius* and *G. personatus* occur in Texas in one of the most arid regions in the range of present day *Geomys*; however, even in that region the average annual precipitation varies from 38 inches to 30 inches (Kennerly 1959: 249-257).

The presence of such browsing animals as *Odocoileus* and *Cervus* (?) permits the probable inference that there must have been wooded areas, at least near the stream margins.

Members of the genus *Geomys* in general seem to be partial to sandy, friable soils (Kennerly loc. cit.). It is likely that this type of soil existed when the Vallecito Creek beds were being deposited, for the specimens of *Geomys garbanii* were collected from that part of the Palm Spring forma-

Table 8

Time distribution of the species of *Geomys*, *Nerterogeomys* and *Zygogeomys* in the Late Cenozoic. [*Geomys bursarius* is represented in the Late Pleistocene by *G. bursarius* from Cragin Quarry, Kansas (Hibbard and Taylor 1960:165) and *G. b. parvidens* from the Conard Fissure.]

Species	Stratigraphic Occurrence			
	Blancan	Irvingtonian	Rancholabrean	Recent
<i>G. bursarius</i>			X	X
<i>G. pinetis</i>				X
<i>G. arenarius</i>				X
<i>G. personatus</i>				X
<i>G. bisulcatus</i>	X?	X?		
<i>G. quinni</i>	X			
<i>G. garbanii</i>		X		
<i>G. tobinensis</i>		X		
<i>Nerterogeomys</i>	X	X?		
<i>Zygogeomys</i>				X

tion characterized by medium to fine-grained sandstones and silts—the type of sediments one would expect in a flood plain deposit.

Summary

A new species of extinct *Geomys* is described from the Western Imperial Valley of Southern California and extensive data are presented on intraspecific variation in Recent and fossil species of *Geomys*.

Certain characters of the new species *Geomys garbanii* are deemed to be primitive and show closer relationship to the heteromyids than to any other *Geomys*. These characters are: opisthodont upper incisors, deep rostrum, large auditory bullae, and large external auditory meatus. Other characters of *G. garbanii* also are deemed to be primitive but their relationships are subtle, for they occur in adult specimens of the fossil species and in juvenal specimens of Recent species. *G. quinni* from the Sand Draw (Blancan) local fauna of Nebraska also has primitive characters that are present in *G. garbanii*.

The structural similarity of extant *G. bursarius* to *G. parvidens* and the late (?Illinoian) occurrence of the latter species from the Conard Fissure fauna of Arkansas, lead us to place *G. parvidens* as a subspecies under *G. bursarius* as *G. b. parvidens*.

Zygogeomys, a genus which occurs in a restricted area in Mexico, resembles *G. garbanii* and is considered to be a relict genus possibly representing the modern survival of the *G. garbanii* structural type.

G. garbanii has been collected from throughout nearly 2500 feet of section in the upper part of the Palm Spring formation, yet no apparent difference exists between specimens taken from higher or lower portions of the section.

Paleoecologically, the presence of *G. garbanii* in the Vallecito Creek fauna indicates some type of grasslands and a moderate, average annual precipitation.

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